

Plasticity of internodes and petioles in prostrate and erect *Potentilla* species

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Summary

1. In phylogenetically related species, internodes of erect and stoloniferous plants are homologous structures, whereas petioles of prostrate plants and internodes of erect plants are structurally analogous, i.e. they have the same ecological function.
2. The hypothesis was tested that analogous spacing organs would show similar degrees of plasticity in response to shading, whereas homologous spacing organs would not. Four closely related *Potentilla* species representing a range of growth forms from strictly erect to obligatory stoloniferous were studied.
3. Vertical spacers showed significantly higher degrees of plasticity than horizontal spacers in response to shading, confirming the hypothesis that analogous organs show a similar response, whereas homologous spacers differed significantly in their plasticity.
4. Under shaded conditions high degrees of elongation in vertical spacers were accompanied by a significant increase in biomass allocation to these organs, whereas allocation to horizontal spacers tended to be less than under unshaded conditions. This result suggests that significant biomass investments are associated with plastic elongation responses.
5. The results of the study are discussed in the context of specific selection pressures acting on different growth forms which may alter the degree of morphological plasticity of plant organs during evolution.

Key-words: Biomass allocation, clonal growth, growth form, light quality, light quantity

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Introduction

Herbaceous plants from open habitats usually show strong morphological responses to shading. In erect herbs one of the most obvious morphological reactions to low light intensities is the elongation of internodes (Mitchell & Woodward 1988; Schmitt & Wulff 1993). This response has been interpreted as a mechanism to position leaves in the upper layer of the canopy, thereby enhancing light harvesting (Grime, Crick & Rincon 1986; Ballaré 1994). The response is triggered through phytochrome and blue-light-absorbing photoreceptors (Morgan & Smith 1979; Ballaré, Scopel & Sánchez 1991). Elongation responses are often less strong if only the light quantity, but not the light quality, is changed (Grime & Jeffrey 1965; Mitchell & Woodward 1988; Schmitt & Wulff 1993; Ballaré 1994).

Elongation of internodes in stoloniferous plants in shaded patches has been regarded as a search–avoid-

ance mechanism, which potentially leads to an accumulation of ramets in high-light patches (Slade & Hutchings 1987a,b; Sutherland & Stillman 1988; Hutchings & Slade 1988; Hutchings & Mogie 1990; Hutchings & de Kroon 1994). However, internode elongation is rarely sufficient to confirm this notion (de Kroon & Hutchings 1995). Clear elongation responses have been reported for *Glechoma hederacea* (Slade & Hutchings 1987a,b), for *Cynodon dactylon* (Dong & de Kroon 1994) and, in a field study, for *Ranunculus repens* (Waite 1994), whereas the internodes of many other species respond little to shading, or show inconsistent responses (Lovett Doust 1987; Sutherland & Stillman 1988; de Kroon *et al.* 1994).

In dicotyledonous species, stoloniferous herbs have been derived from erect ancestors (Goebel 1923; Tiffney & Niklas 1985; Hilligardt & Weberling 1989; Hutchings & Mogie 1990; Krahulec 1994; Serebryakova 1981). As a consequence of this phylogenetic relationship, internodes of plants are homologous organs, regardless of whether their stems are

orthotropic or plagiotropic. Thus, horizontal and vertical axes might respond similarly to shading (Hutchings & Mogie 1990), although direct comparisons of the two growth forms have not been made so far (Silander 1985; Hutchings & Mogie 1990; Ballaré 1994).

Recently, Ballaré (1994) suggested that functionally corresponding (i.e. analogous) organs, rather than phylogenetically corresponding (i.e. homologous) organs, should show similar levels of plasticity in their responses to environmental factors. In herbaceous plants, the internodes of erect plants and the petioles of stoloniferous plants can be regarded as analogous organs, which can be used by the plant as spacers to enhance light harvesting in dense stands of herbaceous vegetation. If high plasticity of vertical spacers is a mechanism to enhance light harvesting, both internodes of erect plants and petioles of stoloniferous plants should respond similarly to shading.

The hypothesis was tested that vertical spacers (i.e. petioles of stoloniferous plants and internodes of erect plants) will show a similar and high degree of plasticity in their responses to shading, whereas these responses need not be of a similar magnitude in homologous organs of plants with different growth forms. This hypothesis was tested in a garden experiment in which four *Potentilla* species with different growth forms were subjected to three light regimes differing in radiation quantity and quality.

Materials and methods

SPECIES DESCRIPTION

The experiment was carried out with the two erect herbs *Potentilla recta* L. and *P. erecta* (L.) Räuschel and the two stoloniferous herbs *P. anglica* Laich. and *P. reptans* L. (Fig. 1). *P. anglica* is a fertile hybrid

species of *P. erecta* and *P. reptans* (Wolf 1908; Matfield, Jones & Ellis 1970; Matfield & Ellis 1972). Serebryakova (1981) has shown that the stolon of *P. reptans* is homologous to the reproductive shoot of *P. erecta* and is thus likely to have evolved from the reproductive shoot of a *P. erecta*-like ancestor.

P. recta occurs in dry, sunny places and occasionally in shrub and forest edges (Hegi 1981). *P. erecta* is widespread in open habitats, especially in grasslands, with a variation of moisture contents. It can also occur in open forests (Hegi 1981). *P. anglica* is mainly found in moist and somewhat shady places such as deciduous forests and fens, or in slightly disturbed habitats such as roadside verges, river shores and the edges of arable fields (Hegi 1981). *P. reptans* has a similar distribution, but it does not occur in forests, and is very common in pastures and highly disturbed habitats (Hegi 1981; Stuefer, During & de Kroon 1994).

THE EXPERIMENT

All four species were grown from material obtained in the Netherlands. Ramets of *P. reptans* were collected in the summer of 1992 in the vicinity of Utrecht. In the early summer of 1993, plantlets of *P. anglica* and *P. erecta* were collected in the vicinity of Eindhoven and in Oostvoorne, respectively. *P. recta* was cultivated from seeds (obtained from the Croidthoek, The Hague, NL), which were sown in June 1993. All four species were grown outside in the Botanical Garden of Utrecht University until the start of the experiment in spring 1994.

In April 1994 fifty individuals of each species were transferred to an open plastic greenhouse (light availability ca. 90% of full daylight). In order to standardize for plant size, all leaves of the selected individuals

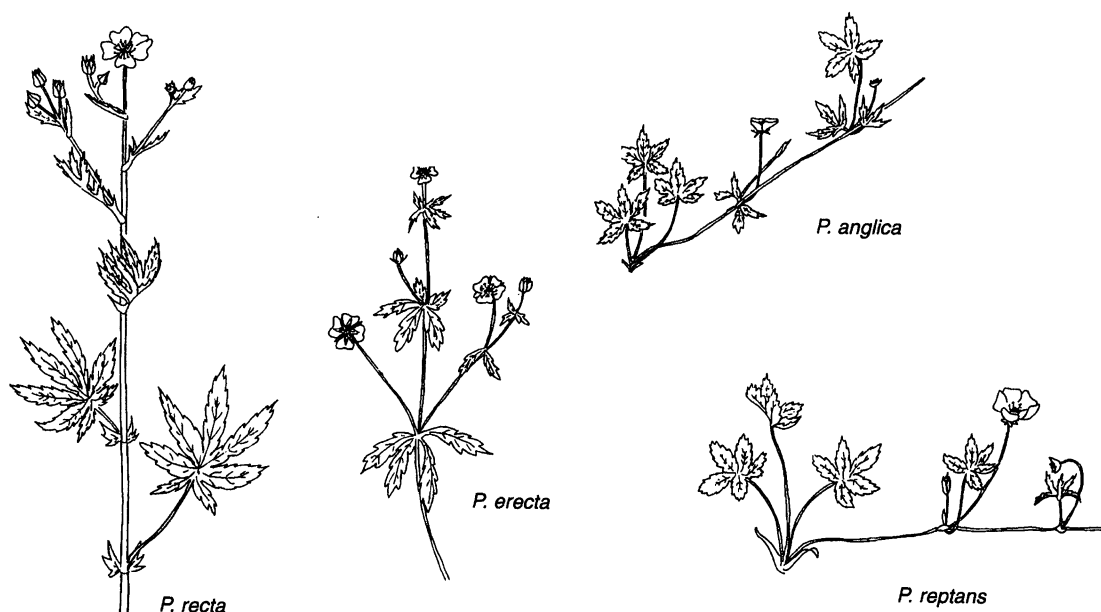


Fig. 1. Schematic illustration of the four *Potentilla* species used in the experiments.

except the three youngest ones were removed, and the roots were cut to a length of 5 cm. *P. recta*, *P. anglica* and *P. reptans* were planted individually in plastic pots (13-cm deep and 13-cm diameter) filled with river sand and 5 g of slow-release fertilizer (Osmocote Plus, Grace Sierra International, Heerlen, the Netherlands). The nitrogen release corresponded to 10 kg ha⁻¹ week⁻¹. *P. erecta* was grown in pots filled with a soil mixture of 1 : 1 sieved potting compost and sand with an addition of 4 g Osmocote because this species, occurring naturally on soils with a very high organic component, shows very poor growth on pure sand. The ramets along the oldest stolon of the two stoloniferous species were rooted in a plastic tray (15-cm deep, 15-cm wide and 100-cm long) filled with river sand. Young ramets along the stolon were supplied with the same amount of nutrients as the mother rosettes. Thirty similar-sized individuals of each species were allocated randomly to the experimental treatments at the beginning of May 1994.

Three treatments were applied with ten replicates each. In two shading treatments, whole plants were grown in shade cages. Neutral shading was achieved by one layer of black shade cloth, which reduced photosynthetic photon flux density (PPFD) to 24% (measured with a Li-185a meter, LiCor, NB) without changing the red : far-red ratio. Spectral shading was imposed by one layer of a plastic film [Lee Colortran International (Andover, UK), no. 122, fern green] which reduced the red : far-red ratio to 0.21. Red : far-red ratios were measured with a remote cosine receptor connected to a spectroradiometer (Licor Li-1800). Fluence rates were measured in the spectral range of 655–665 nm (red) and 725–735 nm (far-red). In this treatment PPFD was reduced to the same value as in the neutral shade treatment. Control plants received 100% PPFD and a red : far-red ratio of 1.09. PPFD values reached a maximum of approximately 1800 µmol m⁻² s⁻¹ on clear days. The control plants were grown in cages surrounded by a thin colourless plastic film in order to make microclimatic conditions comparable between all treatments (Table 1). Throughout the experiment the plants were watered daily with tap water.

Owing to differences in phenological development, the four species were not harvested at the same time. Morphological and allocation-related parameters have been shown to change during ontogeny (Coleman, McConnaughay & Ackerly 1994). Because in the two erect species the development of single modules was

terminated earlier than in the stoloniferous species, the experimental treatments lasted shorter for the erect than for the two stoloniferous species. *Potentilla recta* was harvested after flowering induction had taken place and plants had finished stem elongation. This was four weeks after the start of the experiment. *P. erecta* was also harvested four weeks after the plants had been allocated to the treatments. *P. reptans* and *P. anglica* were harvested when the first stolons had reached the end of the tray, i.e. seven weeks and nine weeks after the start of the experiment, respectively. This harvesting strategy does not allow comparison of absolute production parameters between species. However, care was taken to ensure that the plants were fully grown, to allow comparison of other morphological parameters and allocation patterns between species. At harvest, stem or stolon length, the length and thickness of the internodes, and the length of the petioles of three similar-aged leaves of each plant were measured. Internode thickness was measured with a Dial Thickness Gage (Mitutoyo Cooperation, Japan) with an accuracy of 0.01 mm. Internode and petiole length were measured with a digitalized calliper rule (Helios digit, Overtom International Technics, Den Dolder, the Netherlands) with an accuracy of 0.1 mm. Dry mass of the different organs was determined after drying the plants to constant mass at 72 °C. The main stems or stolons and petioles were dried individually in order to calculate the specific lengths and mass ratios of these organs.

STATISTICAL ANALYSES AND THE MEASUREMENT OF PLASTICITY

Treatment effects were tested by a one-way ANOVA followed by the degree of plasticity in petiole and internode length within and between species was compared with an analysis of variance after applying a log transformation. The use of absolute differences in length in the analyses of plasticity would not be appropriate because these are dependent on the absolute length of an organ. Thus, log transformation was applied to transfer this inherently multiplicative effect into an additive effect, which can be analysed by a standard analysis of variance. This allowed comparison of relative differences of plasticity even if absolute organ size was different. As natural shading results in a change in both light quantity and light quality, the length of spacers of plants grown under full daylight was compared with the length of spacers of spectrally shaded plants in the two following analyses.

To test for differences in the plasticity of petioles and internodes *within one species*, a two-way ANOVA was used, with treatment and organ type as main factors. In this analysis a significant interaction term (organ × treatment) indicates a different response of internodes and petioles to shading.

Table 1. Light quantity (% PPFD) and quality (red : far-red ratio) in the three treatments used

Treatment	% PPFD	r : f-r ratio
Control (C)	100	1.09
Neutral shade (N)	24	1.09
Spectral shade (S)	24	0.21

To test for differences in plasticity of internodes and petioles *between species*, a one-way analysis of variance followed by three planned comparisons was used. These planned comparisons were carried out between *P. recta* and *P. erecta*, *P. erecta* and *P. anglica*, and *P. anglica* and *P. reptans*, representing the gradient in growth form from erect to stoloniferous. The null hypothesis tested was that the difference in (for example) internode length in control conditions and spectral shade was the same in the two species compared. As the three tests performed for each organ matched the assumptions of orthogonality, the null hypothesis was rejected if the value of *P* was lower than 0.05 (Sokal & Rohlf 1981). A rejection of the null hypothesis indicates a different response of the organ being considered in the two species compared. The statistical program package SAS (SAS 1988) was used for all analyses.

Results

INTERNODE AND PETIOLE LENGTH

Generally, internode and petiole lengths were higher under shaded than under high-light conditions (Fig. 2). In the two erect species, *P. recta* and *P. erecta*, internodes elongated significantly more than petioles. In the two stoloniferous species, the elongation of petioles was more pronounced than that of the internodes. In *P. reptans*, petioles were 2–3 times longer in shaded conditions than in high-light

conditions. Although the percentage changes in internode length and in petiole length were different in response to shading in all four species, differences were only significant in *P. reptans* (Table 2).

Plasticity in petiole length was significantly lower in the two erect species than in the two stoloniferous species (Table 2). In the two stoloniferous species, the plasticity of petioles was significantly higher in *P. reptans* than in *P. anglica*. Plasticity of internodes was highest in *P. recta*, followed by *P. erecta* and *P. anglica*. The internodes of *P. reptans* showed no plastic response to shading (Table 2).

Except for the petioles of *P. erecta* and the internodes of *P. reptans*, a reduction of the red : far-red ratio further enhanced the effect of reduced light quantity on the elongation of both spacer types (Fig. 2). This resulted in the shortest internodes and petioles being produced under control conditions, followed by those produced under neutral shade. The longest internodes and petioles were formed under spectral shade.

BIOMASS ALLOCATION

The experimental treatments had significant effects on total biomass in all four species (Table 3). The biomass allocation pattern was also influenced by treatments (Fig. 3) in all species except in *P. erecta*. Root : shoot ratio decreased significantly under shaded conditions. This effect was enhanced when the plants were subjected to a low red : far-red ratio. The relative allocation to stems (i.e. internodes) increased

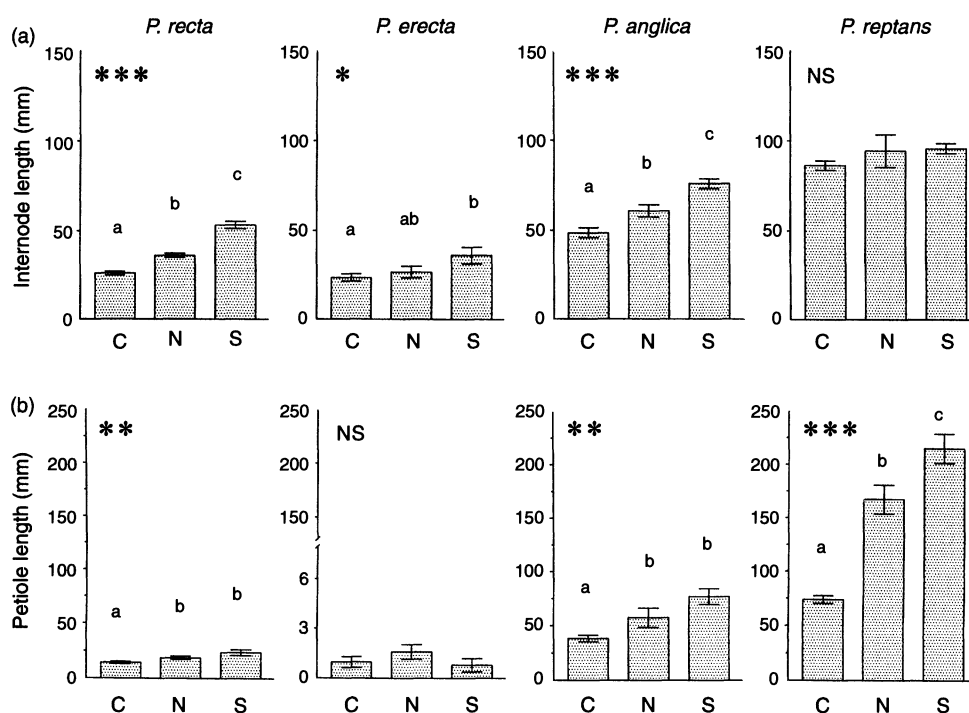


Fig. 2. Mean length (± 1 SE) of (a) internodes and (b) petioles. The result of the one-way ANOVA is given (significance levels: NS, *P* > 0.05; **P* < 0.05; ***P* < 0.01; ****P* < 0.001) in the left hand corner of each graph. Different letters above the bars indicate a significant difference between treatments at *P* ≤ 0.05. Treatment abbreviations: C, control treatment; N, neutral shade; S, spectral shade.

Table 2. Relative increase (as a percentage of the value in the control treatment) of internode and petiole lengths in spectral shade compared with the control treatment. The significance levels next to the species name indicate whether the internodes and petioles differ in their plasticity *within species* (***, $P < 0.001$; NS, not significant). Different letters next to the values indicate differences *between species* in the plasticity of the respective organ at $P \leq 0.05$

Species	Petioles	Internodes
<i>P. recta</i> ^{NS}	66.3 ^a	103.9 ^a
<i>P. erecta</i> ^{NS}	33.7 ^a	53.9 ^b
<i>P. anglica</i> ^{NS}	100.3 ^b	55.8 ^b
<i>P. reptans</i> ^{***}	191.6 ^c	10.8 ^c

under shaded conditions in *P. recta* and decreased significantly in *P. reptans* (Fig. 3).

The relative allocation to leaves and petioles generally increased under shaded conditions. This was most pronounced in *P. reptans* (Fig. 3). In *P. reptans* and *P. recta* the relative allocation to petioles almost doubled under shaded conditions, whereas allocation to leaf blades increased by only 20–50%. The mass ratio of leaf blades to petioles thus decreased under shaded conditions (Table 3).

Petioles were significantly heavier in the two stoloniferous species when grown in shade, whereas the mass of the main axis decreased (Table 3). Both of these changes in mass were more pronounced in *P. reptans* than in *P. anglica*. They were significant in *P. anglica* in only one of the two shade treatments (spectral shade). There was no significant effect of treatments on the average mass of petioles in either of the erect species (Table 3). The stem mass was significantly reduced in neutral shade in *P. recta* and did not differ between treatments in *P. erecta*.

Specific petiole length and specific stem length increased under shaded conditions in all four species (Table 3). The increase in specific petiole length was more pronounced in the two erect than in the two stoloniferous species. In all four species the response in specific petiole length was less pronounced than the response in specific stem length.

Discussion

PLASTICITY OF HOMOLOGOUS VS ANALOGOUS STRUCTURES

In all four *Potentilla* species, internode length, petiole length or both responded significantly to shading.

Table 3. Mean (\pm SE) values for total biomass and various morphological parameters. Different letters next to the values indicate differences between treatments that were significant at $P \leq 0.05$ (NS, not significant). Significance tests were performed individually for each species and each variable

	Control treatment	Neutral shade	Spectral shade
<i>Potentilla recta</i>			
total biomass (g)	6.38 \pm 0.40 ^a	3.97 \pm 0.26 ^b	3.92 \pm 0.22 ^b
specific petiole length (m g ⁻¹)	2.21 \pm 0.09 ^a	2.95 \pm 0.10 ^b	3.17 \pm 0.08 ^b
specific stem length (m g ⁻¹)	0.37 \pm 0.33 ^a	0.64 \pm 0.03 ^b	0.67 \pm 0.03 ^b
leaf blade/petiole mass ratio	21.9 \pm 1.82 ^a	17.6 \pm 1.49 ^b	14.9 \pm 0.65 ^b
petiole mass (mg)	6.49 \pm 0.50 ^{NS}	6.49 \pm 0.60 ^{NS}	7.58 \pm 0.88 ^{NS}
stem mass (mg)	839.9 \pm 65.3 ^a	674.0 \pm 68.9 ^b	906.8 \pm 62.9 ^a
<i>Potentilla erecta</i>			
total biomass (g)	2.06 \pm 0.23 ^a	0.77 \pm 0.16 ^b	0.86 \pm 0.10 ^b
specific petiole length (m g ⁻¹)	12.2 \pm 0.99 ^a	20.7 \pm 1.62 ^b	17.4 \pm 0.74 ^b
specific stem length (m g ⁻¹)	5.65 \pm 0.55 ^a	9.03 \pm 1.11 ^b	9.94 \pm 0.86 ^b
leaf blade/petiole mass ratio	8.21 \pm 1.24 ^{NS}	5.88 \pm 0.66 ^{NS}	6.14 \pm 0.80 ^{NS}
petiole mass (mg)	2.37 \pm 0.34 ^{NS}	1.64 \pm 0.23 ^{NS}	2.11 \pm 0.26 ^{NS}
stem mass (mg)	29.9 \pm 4.90 ^{NS}	16.3 \pm 3.1 ^{NS}	20.6 \pm 5.3 ^{NS}
<i>Potentilla anglica</i>			
total biomass (g)	10.2 \pm 0.77 ^a	2.58 \pm 0.24 ^c	6.04 \pm 0.46 ^b
specific petiole length (m g ⁻¹)	5.40 \pm 0.21 ^a	7.69 \pm 0.36 ^b	6.98 \pm 0.23 ^b
specific stolon length (m g ⁻¹)	1.74 \pm 0.08 ^a	3.47 \pm 0.15 ^c	2.84 \pm 0.18 ^b
leaf blade/petiole mass ratio	4.81 \pm 0.20 ^{NS}	4.11 \pm 0.44 ^{NS}	3.94 \pm 0.24 ^{NS}
petiole mass (mg)	7.35 \pm 0.81 ^a	7.43 \pm 1.39 ^a	11.12 \pm 1.14 ^b
mass of the primary stolon (mg)	392.8 \pm 34.5 ^a	209.5 \pm 15.1 ^b	370.5 \pm 27.3 ^a
<i>Potentilla reptans</i>			
total biomass (g)	11.3 \pm 1.27 ^a	4.22 \pm 0.52 ^b	4.93 \pm 0.28 ^b
specific petiole length (m g ⁻¹)	2.78 \pm 0.14 ^a	3.58 \pm 0.25 ^b	3.26 \pm 0.16 ^b
specific stolon length (m g ⁻¹)	1.28 \pm 0.14 ^a	2.48 \pm 0.14 ^b	2.19 \pm 0.10 ^b
leaf blade/petiole mass ratio	3.87 \pm 0.15 ^a	2.41 \pm 0.11 ^b	2.14 \pm 0.10 ^b
petiole mass (mg)	26.92 \pm 1.51 ^a	50.22 \pm 6.28 ^b	66.64 \pm 6.14 ^c
mass of primary stolon (mg)	989.3 \pm 100.2 ^a	421.3 \pm 51.3 ^b	542.7 \pm 34.6 ^b

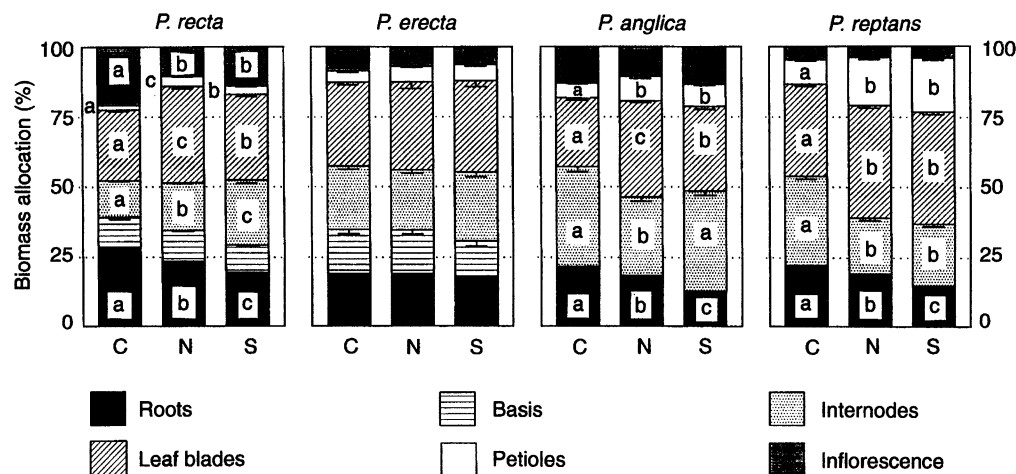


Fig. 3. Proportional biomass allocation to plant organs (\pm 1SE). For treatment abbreviations see Fig. 2. In *P. recta*, 'basis' refers to the lowest, partly below-ground thickened part of the stem, from which the roots and other primary stems originate. In *P. erecta*, 'basis' refers to a below-ground tuber. Different letters indicate a statistically significant difference between treatments at $P \leq 0.05$.

Whereas internodes of plants with vertical stems responded more strongly to shading, petioles exhibited higher degrees of plasticity in stoloniferous plants. This result indicates that homologous organs that differ in their function respond differently to shading. Conversely, different organs show similar degrees of plasticity if they have the same orientation and therefore fulfil similar ecological functions.

In dense stands of herbaceous vegetation there is a strong vertical light gradient, with low light availability at the bottom and increasingly higher light supply in the upper parts of the canopy (Monsi & Saeki 1953; Fliervoet 1984; Hirose & Werger 1995). Elongation of vertical spacers is likely to enhance light harvesting by species in such canopies. These results confirm that vertical spacers show stronger responses to shading than horizontally growing organs, and that homology between organs does not necessarily ensure that they respond similarly to shading. The results do not support the proposition that the internodes of stoloniferous plants show high plasticity owing to their homology with internodes of erect plants (Hutchings & Mogie 1990). However, the results are in agreement with the suggestion of Ballaré (1994) that petioles rather than internodes of stoloniferous plants should elongate under shaded conditions.

In several studies on clonal species, petioles have been found to show considerably more plasticity than internodes (Hutchings & de Kroon 1994, and references therein). In general, internodes show a maximum elongation response of about 30% in shaded conditions (but see Dong & de Kroon 1994), whereas petioles of the same species can be about 100–200% longer in shaded conditions compared with high-light conditions (Hutchings & de Kroon 1994; Dong 1995). These values found for petioles are comparable to values found for internodes in erect plants (Schmitt & Wulff 1993), thereby supporting the notion that

vertically oriented organs are characterized by high degrees of plasticity in response to shade, whereas horizontally oriented spacers are not.

The ability to respond plastically may be related to the time at which an organ elongates (Birch & Hutchings 1992). Whereas internodes of *Glechoma hederacea* complete their elongation after a short time, petiole elongation can be very prolonged and this presumably enables them to respond to changes in local light climate caused by the growth of surrounding vegetation (Birch & Hutchings 1992). In addition, in the present experiment, spacers with a high plasticity elongated over a longer period of time than spacers with low plasticity. In erect plants the petioles of stem leaves elongated only during a few days, whereas elongation of internodes lasted between 10 and 14 days. In the stoloniferous plants the difference in elongation time was less pronounced: as in *P. reptans* the elongation of petioles took only 20–40% longer than the elongation of internodes. This small difference in elongation time may not fully explain the large differences of plasticity in the latter species.

In contrast to the other three species, internodes as well as petioles of the hybrid species *P. anglica* showed high degrees of plasticity, suggesting that this species has inherited the plasticity of internodes from the erect parent plant *P. erecta* and the plasticity of petioles from the stoloniferous parent plant *P. reptans*. However, the petioles were less plastic in *P. anglica* than in *P. reptans* (Table 2).

Plasticity can be altered by selection (Bradshaw 1965; Schlichting 1986; Scheiner 1993). Different selection pressures may explain differences in plasticity between closely related species with different growth forms. According to Scheiner (1993), high plasticity is favoured when the environment is variable but predictable. This means that high plasticity of a trait is likely to be favoured by selection if individu-

als of a population have a high chance of encountering different environmental conditions and if plasticity of a particular trait (e.g. stem elongation in erect plants) enhances the performance of plants. In addition, ramets of stoloniferous plants may happen to grow in patches of different light availabilities. Under these conditions the success of plasticity of petioles of stoloniferous plants is very predictable, as elongation of petioles will in most cases result in higher light uptake of the leaves, owing to the consistent pattern of the vertical light climate in herbaceous canopies. As a consequence, the high plasticity of vertical spacers, i.e. petioles of stoloniferous plants and internodes of erect plants, may be seen as a response to the high predictability of the vertical light gradient in dense patches of herbaceous canopies. On the other hand, the low and inconsistent plasticity of horizontal spacers between species may indicate that variability in light levels is less predictable in the horizontal direction and that, hence, plasticity in the length of horizontal spacers does not necessarily enhance light uptake. Vertically oriented spacers, but not creeping stolons, can also perceive signals that precede increased competition for light with neighbouring plants. The spectral distribution of light received by vertically oriented organs is affected by radiation scattered by the nearby vegetation, even at very low levels of canopy cover (Ballaré *et al.* 1987; Ballaré, Scopel & Sánchez 1989, 1991). Therefore, changes in the light environment sensed by these organs are among the earliest signals of the proximity of encroaching vegetation, and a high responsiveness of vertically oriented organs to these signals would confer a major advantage for the plant. In contrast, the spectral distribution of light received by horizontal organs does not change much with the density of the surrounding vegetation until these organs are actually shaded by foliage (Ballaré *et al.* 1987, 1989). Plasticity of petioles situated on a vertical stem can be interpreted as a potentially efficient response to local canopy conditions, enabling fine-tuning of the positioning of leaf blades to avoid self-shading (Mitchell & Woodward 1988; Ballaré 1994). Biomechanical constraints, however, limit the magnitude of the response (Givnish 1986). Thus, enhanced plasticity of petioles in stoloniferous plants may be seen as a reinforcement of an already present trait.

COSTS OF PLASTICITY

According to several authors (Goebel 1923; Serebryakova 1981; Tiffney & Niklas 1985; Hilligardt & Weberling 1989; Hutchings & Mogie 1990; Krahulec 1994) it can be assumed that in different taxa of the angiosperms, stoloniferous plants are phylogenetically derived from herbs with a vertical stem. In many cases the horizontal stem is homologous to the vertically oriented reproductive shoot of erect species (Goebel 1923; Serebryakova 1981). In combi-

nation with the results presented here, this would suggest that plasticity of internodes as a response to light climate may have decreased during the evolution of stolonifery. Because a trait is only likely to be selected against if the costs of maintaining the trait exceed the benefits associated with it, the question arises whether there are costs associated with high degrees of plasticity in spacer length.

Shading resulted in a species-specific change of biomass allocation patterns. In the erect species *Potentilla recta*, biomass allocation to the stem was significantly increased under shaded conditions. In the stoloniferous species *P. reptans*, on the other hand, shading led to a decreased allocation to stems and a highly increased allocation to petioles (Fig. 3). Hence, elongation of the analogous, vertically oriented organs involved a strongly increased allocation of resources to these organs. This indicates that enhanced elongation carries a cost in terms of the biomass allocated to the elongating organ. In vertical spacers, the benefits associated with the increased elongation of these spacers will more than compensate for the costs. In stoloniferous plants, however, high plasticity of internodes would, owing to the low predictability of horizontal heterogeneity in light availability, not necessarily increase light-harvesting potential, and might thus bring little benefit (Sutherland & Stillman 1988; Oborny 1994; de Kroon & Hutchings 1995). Therefore, maintenance of such plasticity with its associated costs would be unfavourable in these plants.

BIOMECHANICAL CONSTRAINTS

Internodes as well as petioles of all species investigated in this study had a higher specific length when subjected to shaded conditions. This may be interpreted as a mechanism to save resources, as etiolation can lead to the production of longer internodes and petioles without additional resource investment. However, there are biomechanical constraints on etiolation regarding the strength of vertical organs. Petioles and vertical stems have to carry their own weight as well as the weight of the lamina or leaves and reproductive organs, respectively. Thus, a minimum strength of spacers is needed to prevent buckling or breaking (Givnish 1986; Niklas 1993). This leads to a narrow range of plasticity achievable by pure etiolation. If these organs show high degrees of plasticity, investment of additional carbohydrates is needed to ensure that they have the necessary strength. This can be seen in the petioles of *P. reptans*, which were three times as long and twice as heavy in shaded conditions as in high-light conditions. This suggests that a high plasticity of vertical spacers is associated with costs, which are largely due to biomechanical constraints.

The internodes of the stoloniferous species also had a higher specific length in shaded than in high-light conditions because their thickness was reduced.

In *P. reptans* this increase in specific length was not due to etiolation, as internode length was increased in shaded conditions. This indicates that a fundamentally different mechanism may determine the specific length of internodes compared to that controlling the specific length of petioles in stoloniferous plants. Internode thickness may be related to the transport capacity of water. As the internodes of stoloniferous plants have no support function, the specific length of internodes can be increased to a greater extent than the specific length of internodes of erect plants provided that a certain level of transport capacity is maintained. Price & Hutchings (1992) have shown for *Glechoma hederacea* that in plants grown under different nutrient regimes the stolon cross-sectional area was reduced by 40% under nutrient-poor compared with nutrient-rich conditions. This reduction was due to a reduction in the vascular tissue, cortex and pith. However, neither the proportion of the stolon cross-sectional area occupied by vascular tissue nor the number and diameter of the bigger xylem vessels changed. As the smaller vessels contribute only very little to the total amount of transport capacity (Zimmermann 1983) the formation of thinner internodes does not substantially reduce transport capacity. In *P. reptans*, internode thickness was even more reduced than in *Glechoma hederacea* in shaded conditions, as the cross-sectional area was only 27% of the value in high-light conditions. This strong reduction of the cross-sectional area (73%) may lead to a reduced water transport capacity. However, this does not necessarily result in a reduced plant performance, as under low light levels the transpiration rates are usually lower than in full daylight (cf. Larcher 1994).

CONCLUSIONS

Closely related species of the genus *Potentilla* show considerable differences in the plasticity of homologous organs. The differences in plasticity of phylogenetically corresponding spacers can largely be related to different growth forms of the species, and explained by the different ecological functions of the spacers. Functionally corresponding organs showed similar degrees of plasticity; this result suggests that plasticity of spacers can be acquired and lost during evolution. A high level of plasticity of vertically oriented organs may have been selected for because of the high predictability of the vertical light gradient in herbaceous canopies. High plasticity in spacer elongation is associated with potentially high costs in terms of biomass allocation and reduced biomechanical strength of the vertical spacers. However, the benefits due to increased light harvesting potential of the erect spacers seem to outweigh these costs, and this may have led to the selection of high degrees of plasticity in vertical spacer elongation.

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